Journal of the Royal Society of Western Australia, 75: 47-50, 1992

Seed release from *Banksia baxteri* and *Hakea crassifolia* following scrub-rolling and burning

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Manuscript received September 1991; accepted February 1992

Abstract

Seed release patterns were compared for standing and felled plants of two serotinous shrubs, *Banksia baxteri* and *Hakea crassifolia*, including plants of each species burnt 18 days after felling. Standing plants of both species released only a small proportion of their seed store during the 11 month period of the study. Burning resulted in high levels of follicle rupture and seed release for felled *B. baxteri*; felled but unburnt plants did not release significant amounts of seed despite progressive desiccation. *H. crassifolia* follicles on felled stems opened readily after burning, but also opened in the absence of fire. A laboratory study indicated that the rate of follicle opening was strongly related to the severity of drying conditions.

Fuel reduction burning of shrublands in south-western Australia is sometimes preceded by scrub-rolling: both operations may affect the regeneration of shrubland plant species. Seed released from felled stems in the period between scrub-rolling and subsequent burning may be damaged by heat or even incinerated, thereby reducing the seed bank available for regeneration. The potential for such seed losses can be minimised by keeping the period between scrub-rolling and burning short, preferably no more than a few weeks.

Introduction

Many species of Proteaceae from the shrublands of south-western Australia accumulate seed in woody fruits in the canopy of mature plants; such species are termed serotinous (Lamont 1991). This trait is characteristic of a number of species of *Banksia, Hakea, Dryandra* and *Xylomelum* (Bell *et al.* 1987, Bellairs & Bell 1990). Fruit opening and subsequent seed release may be stimulated by a variety of mechanisms that promote desiccation of the abscission zone, including heat, and death of the branch or plant (Lamont 1991). The importance of heat in follicle rupture on serotinous *Banksia* species has been well documented (Gill 1976, Bradstock & Myerscough 1981, Lamont & Cowling 1984, Enright & Lamont 1989a).

Shrublands in south-western Australia are sometimes scrub-rolled in advance of fuel reduction burning. Scrub-rolling facilitates prescribed burning by creating a more continuous fuel-bed and increasing the proportion of dead fuel through the curing of foliage on felled stems. Fires are more readily controlled in scrub-rolled fuels because flame heights are reduced; this is of considerable importance where narrow buffer strips (typically 100-200 m wide) are to be burnt around the perimeter of a bushland reserve.

Seed released from follicles on felled stems in the period between scrub-rolling and subsequent burning may be damaged by heat or even completely incinerated, thereby reducing the quantity of seed available for regeneration (Richardson & van Wilgen 1986). This may lead to a decline in the population density of species that do not resprout after fire or maintain a seed store in the soil. Knowledge of seed release characteristics is therefore valuable for identifying species which may be vulnerable to this type of disturbance.

We studied seed release from two serotinous shrubs that commonly occur together in shrubland communities on the southern sandplain of Western Australia. *Banksia baxteri* R. Br. produces squat cones with up to 6 follicles, each containing two seeds (George 1981). Florets may persist on cones for several years after maturity. *Hakea crassifolia* Meissn. has a spherical woody follicle about 5 cm in diameter that splits symmetrically, releasing two seeds with membranous wings. The aim of the study was to compare the rate and extent of follicle opening and seed release on felled stems of these two species, both with and without the influence of fire; a control group of standing, unburnt plants were also examined. Such information provides a basis for management guidelines designed to maintain seed banks of serotinous species in scrub-rolled buffer strips.

Methods

The study was undertaken in mallee heath shrubland (Beard 1979) near Two Mile Lake (34°29′ S, 118°15′ E) in the Stirling Range National Park, Western Australia. The area experiences a mediterranean climate with cool moist winters and warm dry summers. At Mt Barker, about 55 km south-west of the site, mean daily maximum and minimum temperatures are 27.2 °C and 13.5 °C respectively in the hottest month (January), and 14.7 °C and 6.4 °C respectively in the coldest month (July). Mean annual rainfall is 472 mm at Kojaneerup, about 10 km from the study site. The area selected for study had been unburnt for 20 years and was dominated by 2-3 m tall thickets of *B. baxteri* with scattered 3-4 m tall *H. crassifolia*, both species growing as open-branched shrubs.

A 100 m wide strip was scrub-rolled through part of the site on 21 March 1989 (Day 0); within this strip a 0.25 ha plot was demarcated and excised from later burning operations. During the initial assessment on 30 March (Day 9) we selected felled plants of *B. baxteri* (10 in the main strip, 10 in the excised plot) and *H. crassifolia* (2 in the main strip); the low density of the latter species at the site prevented more extensive sampling. Standing shrubs of *B.*

Table 1
Numbers of plants, cones and follicles for *B. baxteri* in each treatment.

Treatment	No. of plants	No. of cones	Total No. of follicles
Standing	8	41	116
Felled/unburnt	10	43	93
Felled/burnt	10	39	83

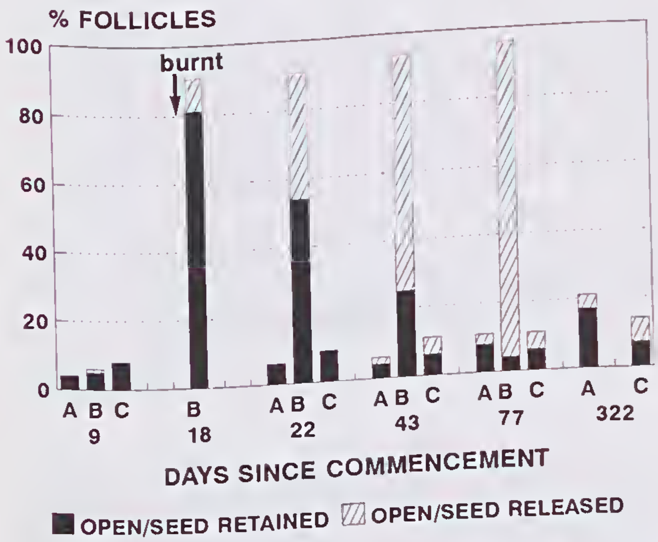

Figure 1 Condition of follicles on *B. baxteri* cones for three treatment groups: (A) felled/unburnt, (B) felled/burnt, and (C) standing/unburnt. Scrub-rolling took place on Day 0. Felled/burnt plants were examined two hours after burning on Day 18.

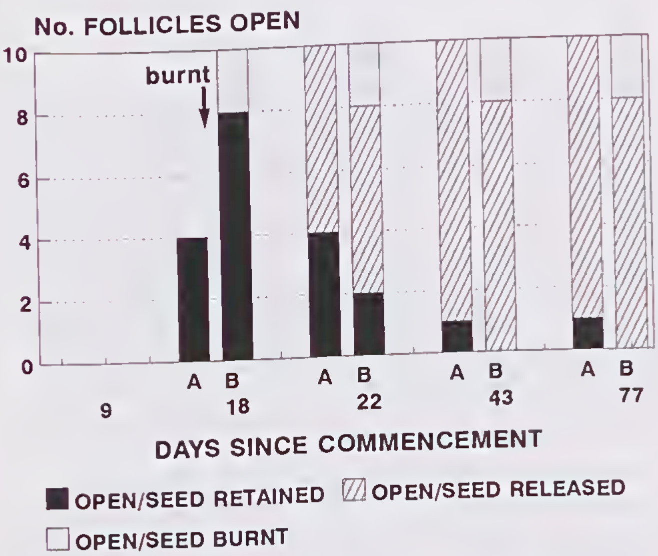

Figure 2 Condition of follicles on felled stems of *H. crassifolia*: (A) for the stem with the intact root system, and (B) for the severed stem. On Day 18 follicles were examined two hours after burning.

baxteri (8) and *H. crassifolia* (2) were also selected in the adjacent untreated area. Each of the *H. crassifolia* plants carried ten mature, unopened follicles at the commencement of the study. One-year-old *B. baxteri* cones on each stem were identified with numbered aluminium tags and the condition of individual follicles described; if open, note was made as to whether the seed was retained or released. Numbers of cones and follicles for each treatment group are shown in Table 1.

The main scrub-rolled strip was burnt during mild conditions on 8 April (Day 18) at about 1500 hrs. About 90% of the ground litter and foliage on felled stems was consumed by the fire which generated intensities (Byram 1959) of 300-500 kW/m. The condition of individual follicles on felled stems within this strip was examined 2 hours after burning, and a small number that had not been burnt were excluded from further study. Plants in all treatment groups were examined again on Day 22 and then at approximately monthly intervals until June when assessment of plants in the burnt strip ceased because seed release was largely complete. Final assessment of plants that had been felled but not burnt, and those in the undisturbed area took place in February 1990 (Day 322).

In October 1990, 28 *B. baxteri* cones were collected at random from each of the standing and felled/unburnt groups of plants. Seed was extracted by heating the cones with a blowtorch to open the follicles, and the seed collected was then placed on moistened vermiculite in petri dishes and maintained at 12-15 °C. The number of germinants was scored after 50 days.

To supplement the limited field data on the opening of *H. crassifolia* follicles in the absence of fire, samples of 23 follicles were dried in the laboratory under three regimes of temperature (T, °C) and relative humidity (RH, %), as follows:

(A) T=35, RH=20
(B) T=25, RH=40 and
(C) T=15, RH=60.

Treatments were imposed within 24 hours of follicles being harvested in the field.

Results

B. baxteri

At the commencement of the experiment more than 90% of the follicles in each treatment group were closed, and the small proportion that were open generally still contained seed. The scrub-rolling operation resulted in the complete severing of the root systems on all felled *B. baxteri*, a reflection of the brittle character of stem tissues.

Fire stimulated the rupture of follicles, and within 2 hours of being burnt more than 90% of follicles on felled stems had opened (Fig 1). By Day 77, fifty nine days after burning, the proportion of follicles opened had increased to 96%. The small number that failed to open typically showed signs of damage by cockatoos and insect borers. Seed was progressively released from opened follicles between April and June and less than 5% of open follicles still retained seed by Day 77 (Fig 1).

By contrast, few follicles on unburnt cones opened between March 1989 and February 1990, irrespective of whether the cones were on standing or felled stems (Fig 1). At the completion of the experiment the proportion of opened follicles on cones in the felled treatment (21%) was not significantly different from that of standing trees (14%) (Chi squared = 1.87, $P > 0.05$).

The number of intact seeds recovered from cones collected in October 1990 was relatively low, with mean numbers of seeds/cone of 0.8 and 0.7 respectively for felled and standing treatments. The proportion of successful germinants from cones on felled stems (15 out of 22 seeds) was lower than from cones on standing trees (19 out of 20 seeds) although this difference was not significant at the 0.05 level (Chi squared = 3.30, $0.10 > P > 0.05$).

H. crassifolia

The roots of one felled *H. crassifolia* plant were fully severed from the stem, while the other plant retained an almost intact root system embedded in the soil. Two follicles on the plant with the severed roots had opened by the time that the scrub-rolled strip was burnt on Day 18, with the result that the seed was incinerated inside the follicle (Fig 2). The remaining eight follicles on this stem opened within 2 hours of being burnt, and seeds were released progressively over the next 25 days. All follicles on the plant with the intact root system remained closed until after the fire and only four opened within 2 hours of being burnt (Fig 2). The remaining six follicles opened during the following 4 days, and seed was released from all but one capsule within 25 days of burning. Between March 1989 and February 1990 only 1 of the 20 follicles on the standing plants opened.

In the laboratory, the rate at which capsules opened depended on the severity of the drying regime (Fig 3). Under the most severe régime (T=35, RH=20) all follicles opened within 5 days; the intermediate regime (T=25, RH=40) resulted in 96% opening within 7 days; the solitary follicle that failed to open had been damaged by insect borers. Follicles did not begin to open until after 7 days under the mild drying regime (T=15, RH=60), and only about 70% had opened at the completion of the 27 day monitoring period. The rate of follicle opening was significantly different for each treatment (Kolmogorov-Smirnov two sample test, $P < 0.01$).

Discussion

Lamont (1991) has drawn attention to the need to distinguishbetween the duration of on-plant seed storage, and the mechanism of seed release. He argues that serotiny should be accepted as the technical term for canopy seed storage, and proposes a series of additional terms to describe various mechanisms of seed release. The importance of the distinction between seed storage and release mechanisms is clearly evident in the case of *H. crassifolia* and *B. baxteri*. Both species accumulate canopy-stored seed and can be regarded as serotinous; however differences in seed release characteristics could potentially result in scrub-rolling and fire treatments having quite different impacts on the population of each species.

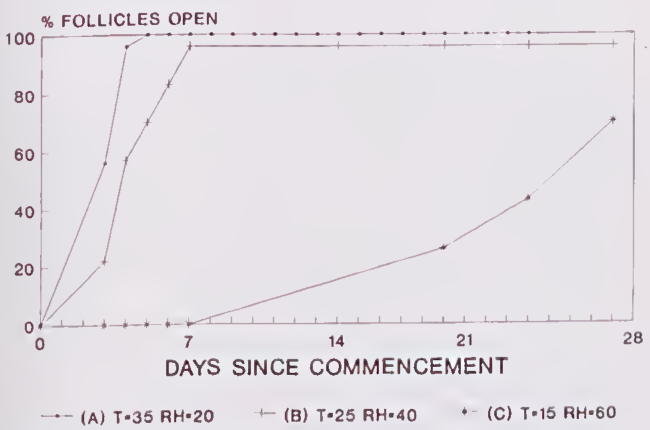

Figure 3 Rate of opening of harvested *H. crassifolia* follicles dried at three regimes of temperature (T, °C) and relative humidity (RH, %) in the laboratory: (A) T=35 RH=20, (B) T=25 RH=40, and (C) T=15 RH=60. Each treatment group consisted of 23 mature follicles.

Fire appears necessary to ensure synchronous follicle opening on *B. baxteri* cones, although a small proportion of follicles will open in the absence of such stimulus. Undisturbed plants exhibited low levels of follicle opening (6%) over the eleven month period of the study, and felling alone did not significantly increase the extent of follicle opening, despite the progressive desiccation of the felled stems. Witkowski *et al.* (1991) have studied seed bank dynamics in a population of *B. baxteri* near the coastal settlement of Hopetoun, some 180 km further to the east. They reported that on undisturbed plants the proportion of open follicles ranged from about 3% on 1-year-old cones to 6% on 8-year-old cones; burning stimulated more than 90% of follicles to open. They also reported that 28% of follicles opened on unburnt cones harvested and placed on the ground, a somewhat larger proportion than the 21% observed for scrub-rolled plants in this study.

In contrast, opening of *H. crassifolia* follicles was not dependent on fire *per se*, but rather on desiccation resulting from death of the plant, or severing of the follicle from the stem. This was clearly illustrated in the laboratory study where the rate of follicle opening was directly related to the severity of the drying regime. Additional evidence of the dependence on dessication can be found in the field study where follicle opening was delayed for the stem with the incompletely severed roots. Lamont (1991) has proposed the term necriscence to describe the phenomenon of seed release following the death of the seed enclosure, as exhibited by *H. crassifolia*.

Serotiny is a common trait in the genus *Banksia* with 76% of species regarded as serotinous (George 1981). Cowling & Lamont (1985a) examined populations of three *Banksia* species along a climatic gradient which extended 500 km north from Perth on the northern sandplain, and concluded that the degree of serotiny was related to the environmental characteristics of the sites where each occurred; strongly serotinous species were most common in scrub-heath communities on xeric sites. However, Witkowski *et al.* (1991) found that the degree of serotiny of *B. baxteri* and *B. speciosa* on the southern sandplain was high compared with non-sprouting *Banksia* species from the northern sandplain, and concluded that serotiny was not necessarily greater in the drier northern region. The overall extent of canopy seed storage for plant communities in south-western Australia has been found to be negatively correlated with annual rainfall (Bellairs & Bell 1990).

Fire is a characteristic feature of the southern sandplain environment due to the protracted summer drought and the high incidence of lightning strikes (McCaw *et al.* 1992). Serotiny has been interpreted as an adaptation to periodic disturbance by intense, stand replacement fires. Synchronous release of a large store of seed from the canopy may be advantageous because favourable seed bed conditions can be fully exploited (Enright & Lamont 1989b), and seed predators may be satiated by the abundant quantities available (O'Dowd & Gill 1984). Witkowski *et al.* (1991) have proposed several explanations for the co-existence of populations of weakly serotinous species such as *B. coccinea* with strongly serotinous species such as *B. baxteri*: recruitment of seedlings of the weakly serotinous species could be significant in the interval between fires; alternatively, fires could co-incide with the period of peak seed production by *B. coccinea* (age 16 to 20 years) prior to decline of the population.

Management Implications

Where fuel-reduced buffer strips are to be established in plant communities containing *B. baxteri* and *H. crassifolia*, or a combination of other species with equivalent seed release characteristics, potential seed losses will be minimised by burning within a few weeks of scrub-rolling. The results of the laboratory study provide an indication of the rate of follicle opening expected for *H. crassifolia* under different drying conditions; factors that may tend to delay follicle opening in the field situation include diurnal variation in temperature and relative humidity, and the continued attachment of seed capsules to felled stems retaining an intact or only partially-severed root system. Weather conditions in the period following scrub-rolling will clearly have an important influence on the rate of follicle opening. Late autumn and early winter conditions are generally favourable for seed release (Cowling & Lamont 1985b) and germination (Bell *et al.* 1987, Enright & Lamont 1989b) by a range of species. Scrub-rolling operations would therefore best be scheduled in early autumn so that seed capsules on felled stems are not exposed to prolonged drying at high temperatures during the summer.

The results of this study further emphasise the important role of fire in stimulating follicle rupture in strongly serotinous *Banksia* species. Scrub-rolled areas containing a significant component of such species will require burning in order to ensure seed release is sufficient to ensure regeneration. For similar reasons, burning may also be appropriate in *Banksia* stands where a high proportion of plants have been killed by disease or insect attack. Management of degraded native plant communities is potentially an issue of profound importance in south-western Australia due to the impact of fungal diseases, particularly those caused by soil-borne species of *Phytophthora* and air-borne canker organisms. A number of serotinous *Banksia* species occur in plant communities threatened or currently seriously affected by disease.

Acknowledgements: We thank John Neal and Joanne Healey for assisting with field and laboratory work. Comments on a draft manuscript were kindly provided by Dr Malcolm Gill, Dr Ian Abbott, Dr Ray Wills and two anonymous reviewers.

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